

A review of the serranochromine cichlid fish genera *Pharyngochromis*, *Sargochromis*, *Serranochromis* and *Chetia* (Teleostei: Labroidei)

PETER HUMPHRY GREENWOOD

Visiting Research Fellow, Zoology Department, The Natural History Museum, Cromwell Road, London SW7 5BD; Honorary Associate, J.L.B. Smith Institute of Ichthyology, Private Bag 1015, Grahamstown 6140, South Africa.

CONTENTS

Introduction	33
Methods and Material	34
Serranochromine taxonomy	36
Introduction	36
The generic or subgeneric status of <i>Serranochromis</i> Regan, 1920, and <i>Sargochromis</i> Regan, 1920, reconsidered	36
The genus <i>Chetia</i> Trewavas, 1961	38
The genus <i>Pharyngochromis</i> Greenwood, 1979	39
Conclusion	40
The phyletic relationships of the serranochromines	40
Generic key and diagnoses	41
Acknowledgements	43
References	43

SYNOPSIS. Recent taxonomic changes, newly described taxa and groups of taxa, and the introduction of taxonomic characters not previously employed require a revision of the informally recognised, essentially fluviatile group of southern African cichlids, the so-called serranochromines. The genera included in this assemblage are *Pharyngochromis*, Greenwood, *Sargochromis* Regan, *Serranochromis* Regan, and *Chetia* Trewavas.

Previously, *Sargochromis* was considered to be a subgenus of *Serranochromis*, but new evidence indicates that it should be reinstated as a distinct lineage (*i.e.* genus). The species originally described as *Serranochromis* (*Sargochromis*) *gracilis* should now be transferred to the genus *Chetia*. Formerly the latter taxon was thought to be monotypic, but it is now expanded to include five species. One of these, *Chetia brevis* Jubb, had been included tentatively in the genus *Astatotilapia*, but is now returned to the genus in which it was described originally.

The monophyletic origin of the serranochromines has still to be established. For that, and other reasons, doubt is cast on the phylogenetic reality of the '*Pharyngochromis* – *Chetia* – *Serranochromis*' group of endemic species in Lake Malawi. The suggested interrelationships of the serranochromine genera presented below, and based on shared derived characters, cannot, for the same reasons, be considered a truly phylogenetic one.

INTRODUCTION

In a paper (Greenwood, 1979) reviewing and reconsidering the generic classification of several cichlid taxa then referred to the genus *Haplochromis*, an informal group of three genera was recognised on the basis of its constituent species having particular types of squamation and anal fin markings (*op. cit.*: 229–316). The group was, and still is considered one of convenience because no cladistically based hypothesis could be erected to establish the monophyly of its contained genera, *viz.* *Serranochromis* Regan, 1920 (with which was incorporated, as a subgenus, *Sargochromis* Regan, 1920), *Chetia* Trewavas, 1961, and *Pharyngochromis* Greenwood, 1979. A scheme of possible interrelationships of these taxa,

suggested earlier by Trewavas (1964), was also discussed in my 1979 paper.

Recent studies of the genera call for a revision of the group's taxonomy at the generic level, and a reconsideration of their possible interrelationship. For example, the genus *Chetia*, treated as monotypic by Greenwood, (1979) is now thought to contain five species (Balon & Stewart, 1983; Greenwood, 1984, 1992, and below, p. 38), certain problems regarding the generic classification of several Angolan haplochromine species have been clarified (Greenwood, 1979, 1984 & 1992), new ideas on the supposed relationship of *Serranochromis* and *Sargochromis* have been put forward by Lippitsch (1991: 99–100), and Eccles & Trewavas (1989: 21) have formally recognised, amongst the endemic genera of Lake Malawi, a large assemblage of species which they

designate 'The *Pharyngochromis* – *Chetia* – *Serranochromis* group'.

The term 'serranochromine' will be used in this paper as a group name for the genera *Chetia*, *Serranochromis*, *Sargochromis* and *Pharyngochromis*. Its use should not be construed as an indication or even a presumption of the group's ultimate and formal recognition as a Tribe. In the sense employed here it is comparable with my earlier use of the informal categories 'haplochromines' and 'pelmatochromines' (Greenwood, 1979 & 1987). Such continued use, and introduction, of informal groupings clashes with the tribal status given by Poll (1986) to several cichlid assemblages in Lake Tanganyika, and with the geographically and taxonomically more extensive tribe Haplochromini defined by Eccles & Trewavas (1989), a tribe which also includes the serranochromines. In my view, these authors' actions are premature. Too few critical higher-level taxonomic studies have yet been made on the Cichlidae to support the phylogenetic relationships that are (or should be) implicit in the award of formal tribal status. For instance, Eccles & Trewavas (1989: 21) define the Haplochromini as: "Maternal mouth-brooding cichlid fishes of Africa and the Jordan Valley in which the basioccipital bone participates with the parasphenoid to form the apophysis for the upper pharyngeal bones". The value of the apophyseal character has been questioned by several authors (see review in Greenwood, 1978, also Greenwood 1986) and it may have evolved more than once among African taxa (Greenwood, 1987); maternal mouthbrooding has apparently evolved independently in both the Tilapiini and Haplochromini (the tribes, respectively, *sensu* Trewavas, 1983, and Eccles & Trewavas, 1989), and in one species of the genus *Chromidotilapia* of the pelmatochromines (*sensu* Greenwood, 1987: 169) in which paper it is also argued (*op cit*: 194–199) that this group should not be included, as it was by Trewavas (1983), in the tribe Tilapiini.

Thus, the purpose of the present paper is simply to clarify the taxonomic status of the 'serranochromine' genera, and to establish a basis for further and phylogenetic studies of those taxa and those of Lake Malawi.

METHODS AND MATERIALS

ANAL FIN SPOTS AND TRUE OCELLI. One of the features used to define the serranochromines is the presence of maculae on the anal fin, usually in both sexes (Greenwood, 1979). A distinction was made there between true ocelli (such as occur, but almost exclusively in males, in a large number of haplochromine species, e.g. those in Lakes Victoria, Edward and Kivu), and the spots or maculae found in the serranochromines and the haplochromines of Lake Malawi (see figure in Eccles & Trewavas, 1991). Judging by a recent description of a new *Serranochromis* species (Winemiller & Kelso-Winemiller, 1991) it is clear that some confusion still exists when discriminating between these two kinds of anal fin markings. Granted, it is often difficult to do so when only preserved material is available, but in life the difference is obvious, as colour photographs in aquarium books will show (e.g. Konings, 1991).

The densely pigmented ovoid or near circular centre of the true ocellus, usually circumscribed by a narrow, darkly pigmented ring, is surrounded, or almost surrounded, by a zone of virtually transparent, or at least freely translucent, and

apparently unpigmented fin membrane. This clear zone is of variable width and outline, but is often concentric with that of the pigmented centre. In life, the clear zone seems to emphasise the coloured central area, thereby making it stand out from the rest of the fin membrane, be that membrane pigmented or hyaline. In colour photographs of live or freshly dead specimens, the clear zone often appears to be dark or even black, a result either of the dark background against which the fish was posed, or the shadow cast by the fish's body and the anal fin itself. To the best of my knowledge, true ocelli do not occur, at least in nature, on any of the other paired fins, although these fins are often maculate. Anal ocelli are also of rare occurrence in females, but large non-ocellate spots are sometimes present on that fin in the females of species whose males have true ocelli. The spots in such females occupy the same position as the ocelli in males, and are often of the same size. As compared with maculae (*i.e.* non-ocellate spots) on the anal fin, true ocelli are generally larger, and are always readily distinguishable from the maculae on the other unpaired fins.

In contrast, non-ocellate anal spots, besides usually being smaller than ocelli, are, with few exceptions (see Greenwood, 1992) more numerous and differ little in their overall appearance from those on the other fins, although the central pigmented portion may differ quite markedly in colour. The essential difference between maculae and ocelli, however, lies in the absence of a transparent or freely translucent area surrounding the pigmented centre of a macula, which, like that of an ocellus, is bounded by a very thin ring of dark pigment. Instead, the macula's pigmented centre is circumscribed by a ring, usually narrow, of lighter pigment which separates it from whatever ground colour the fin membrane may have.

This outer, lightly pigmented ring is not visible in some of the preserved serranochromine specimens I have examined, and the central spot is bounded only by the very narrow ring of dark pigment separating it from the chromatophores in the fin membrane. Whether or not this situation is a preservation artefact cannot be determined at present.

In their account of the anal fin markings in the newly described species *Serranochromis altus*, Winemiller & Kelso-Winemiller (1991: 679) describe, unfortunately without an illustration, the fin in both sexes as having "...30–40 large pink or pink-orange ovate spots, each ringed with a transparent, white ocellus. . .". I would suggest that the use of the words 'transparent and white' in apposition is somewhat contradictory, and that 'translucent white' would describe the condition more accurately, especially since it is one I have seen in fresh specimens of *Serranochromis* (and *Sargochromis*) species from the Okavango river and swamp system in Botswana.

PRESHANK LENGTH OF THE MAXILLA; LENGTH OF THE PRE-MAXILLARY ASCENDING AND ALVEOLAR PROCESSES. The preshank length of the maxilla, relative to its shank length, and the length of the alveolar process of the premaxilla relative to the length of the entire ascending premaxillary process, are two morphometric characters not used in earlier papers (Greenwood, 1979, 1989, 1981).

Preshank length of the maxilla is measured, on the bone's medial aspect, from the anterior tip of the medial arm of the maxilla's saddle process, to the mid-point of the anterior vertical projection from the upper margin of the bone's shank (see Fig. 1). Shank length is measured, also directly and on

the bone's medial aspect, from the midpoint of the vertical projection to the posterior point on the maxilla's posterior margin (see Fig. 1).

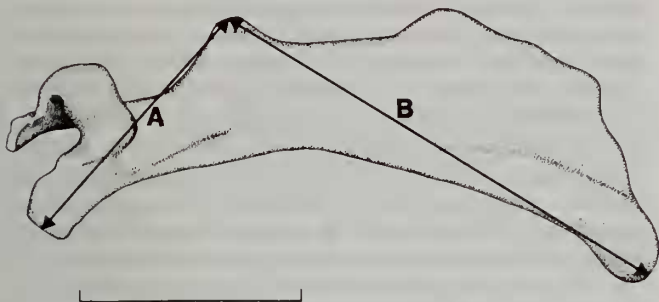


Fig. 1. Medial aspect of maxilla (from *Serranochromis macrocephalus*), viewed somewhat dorsolaterally, to show points of measurement for: A, preshank length, and B, shank length. Scale bar = 5 mm.

The length of the premaxilla's ascending process is measured, directly, from the dentigerous surface of the bone at its symphysis with the premaxilla of the opposite side, to the dorsal tip of the process. The length of the alveolar process uses the same ventral (*i.e.* dentigerous surface) reference point; its dorsal limit being the highest point on the dorsal margin of the process (see Fig. 2).

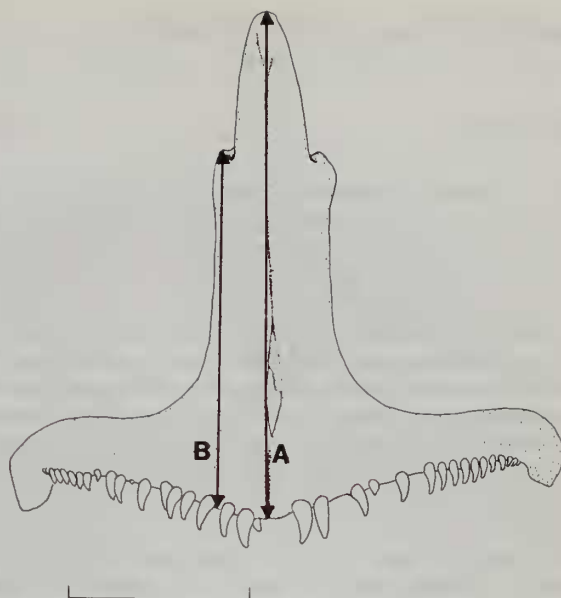


Fig. 2. Frontal view of left and right premaxillae (from *Serranochromis macrocephalus*) to show points of measurement for: A, height of ascending process, B, height of alveolar process. Scale bar = 5 mm.

STUDY MATERIAL

See Greenwood (1979, 1984, 1992) for specimens used in previous studies of *Serranochromis*, *Sargochromis*, *Chetia* and *Pharyngochromis*. Additional material:

- Sargochromis coulteri* RUSI 26627. Namibia (4 specimens)
- Sargochromis coulteri* RUSI 36419. Namibia (1 specimen)
- Sargochromis coulteri* RUSI 28106. Namibia (1 specimen)
- Sargochromis giardi* RUSI 35782. Zambia (3 specimens)
- Sargochromis carlottae* RUSI 31204 Namibia (3 specimens)
- Sargochromis carlottae* RUSI 31214 Namibia (2 specimens)
- Sargochromis coulteri* RUSI 31199. Namibia (1 specimen)
- Serranochromis robustus* RUSI 31169. Botswana; Okavango river (1 specimen)
- Serranochromis thumbergi* RUSI 22660. Dam, Empangeni area, Natal R.S.A. (1 specimen presumably an introduction)
- Serranochromis longimanus* RUSI 23877. Botswana; Okavango swamps (6 specimens)
- Serranochromis macrocephalus* RUSI 24175. Botswana; Boro river (9 specimens)
- Serranochromis angusticeps* RUSI 26854. Okavango swamps (4 specimens)
- Chetia brevis* Holotype AMG. P. 951. Lomati river, R.S.A.
- Chetia brevis* Paratypes AMG. P. 952. Lomati river, R.S.A. (5 specimens)
- Chetia brevis* AMG. P. 1422. Lomati river, Barbeton district, R.S.A. (3 specimens, one partly skeletonized; see below)
- Chetia flaviventris* AMG. P. 1298. Mogel river, Waterberg, R.S.A. (7 specimens, one partly skeletonized; see below)
- Chetia flaviventris* AMG. P. 6871. Tweeport, Rustenburg district, Limpopo system, R.S.A. (10 specimens)

Chetia flaviventris Palala river at Muisvogelkraal (24° 00'S, 28° 24' 30"E) R.S.A. (5 specimens)

Chetia mola Holotype. ROM 29825. Luonga river (Zaire drainage), Zambia

Skeletal material

- Pharyngochromis acuticeps* RUSI 36553. Okovango river (see also Greenwood, 1992)
- Sargochromis carlottae* RUSI 31204. Namibia
- Sargochromis carlottae* RUSI unregistered. 142 mm S.L.
- Sargochromis giardi* RUSI unregistered 210 mm S.L.
- Sargochromis giardi* RUSI unregistered 244 mm S.L.
- Sargochromis cf Sargo. greenwoodi* RUSI unregistered
- Serranochromis macrocephalus* RUSI 24175. Botswana, Boro river
- Serranochromis macrocephalus* RUSI unregistered 107 mm S.L.
- Serranochromis macrocephalus* RUSI unregistered 220 mm S.L.
- Serranochromis macrocephalus* RUSI unregistered ca 220 mm S.L.
- Serranochromis angusticeps* RUSI unregistered 220 mm S.L.
- Serranochromis angusticeps* RUSI unregistered 230 mm S.L.
- Serranochromis angusticeps* RUSI unregistered 410 mm S.L.
- Serranochromis longimanus* RUSI unregistered 150 mm S.L.
- Chetia flaviventris* AMG P. 1298. Mogel river, Waterberg, R.S.A.
- Chetia brevis* AMG P. 1422. Lomati river, R.S.A.

Institutional abbreviations:

- AMG: Albany Museum, Grahamstown
- ROM: Royal Ontario Museum, Toronto
- RUSI: J.L.B. Smith Institute of Ichthyology, Grahamstown

SERRANOCHROMINE TAXONOMY

Introduction

In their revision of certain haplochromine genera from Lake Malawi, Eccles & Trewavas (1991: 21) divide the non-tilapiine taxa of that lake into three groups, one of which they call the *Pharyngochromis* – *Chetia* – *Serranochromis* group. That action I consider to be premature, both because there is little concrete information available about the phyletic inter- and intrarelationships of the Malawi species, and because, as Eccles & Trewavas point out, there are differences between the squamation of those species and that of the serranochromines as construed in this paper (see p. 40). Granted, I have suggested (Greenwood, 1979: 314) that *Serranochromis*- and *Chetia*-like taxa could have been involved in the origin of the Malawian cichlid flocks, but that idea was not put forward on the basis of characters constituting a testable hypothesis. Rather, it was intended, because of the superficial resemblance between the two groups, to promote an awareness that possible intergroup synapomorphies should be looked for in future research.

As recognised in this paper, the serranochromines are an assemblage of mainly fluviatile taxa whose geographical range encompasses the Zambezi, Save-Runde, Limpopo, Cunene, Quanza, Okavango and Zaire river systems, with one species (*Serranochromis robustus robustus* [Günther]), occurring in Lake Malawi (see Balon & Stewart, 1983; Bell-Cross, 1975; Eccles & Trewavas, 1989; Greenwood, 1984, 1992; Jubb, 1967, 1968; Ladiges, 1964; Poll, 1967; Skelton, 1993; Trewavas, 1961, 1964).

Since the last published inventory of serranochromine species (Greenwood, 1979), revisional studies (Greenwood, 1984, 1992) and the description of new species (Balon & Stewart, 1983; Winemiller & Kelso-Winemiller, 1991, and Greenwood, 1984 [see p. 38 below]) have both increased the number of included taxa and extended the geographical range of the group.

Morphologically, the two distinguishing features of the serranochromines are the following. (i) The presence, often in both sexes, of non-ocellate maculae (see p. 34) on the anal fin. Generally these spots are very numerous with, in certain species, as many as 30–40 covering almost the entire fin. However, their number and size show considerable intraspecific (and intergeneric) variability, with as few as three or four large spots occurring in some individuals of a species where the maximum number is 18–20 (Greenwood, 1992). When many spots are present their arrangement may give the impression of an irregular distribution on the fin, but (as was noted by Oliver [1984], *pace* Greenwood, 1979: 315) there is a basically linear regularity in their arrangement. (ii) All scales above the lateral-line series are cycloid, as are the majority of scales below that level. Some weakly ctenoid scales may occur anteriorly on the flanks, especially in small specimens, the ctenii being confined to a narrow arc situated near the centre of the scale's free margin.

A third but less trenchant feature of the serranochromines, as compared with other fluviatile non-tilapiine and non-pelmatochromine taxa (both *sensu* Greenwood, 1987: 194–199) is a tendency for there to be a higher modal number of abdominal vertebrae (modes 16 or 17 in serranochromines, [but 14 in one taxon] cf 12 or 13 in the other taxa); however,

the ranges for total vertebral counts in the two groups overlap.

Where information is available on breeding habits, the serranochromine species are known to be female mouth-brooders, and in all taxa the neurocranial apophysis for the upper pharyngeal bones is formed from the parasphenoid and the basioccipital bones. In those respects, the group would conform with Eccles & Trewavas' (1989) definition of the tribe Haplochromini.

Recently, Lippitsch (1991) drew attention to the possible value of scale morphology and patterns in resolving certain problems of intergeneric relationships within the serranochromines. To determine if the features described by Lippitsch could also provide another 'group' characteristic, I examined, at a magnification of 50x, the superficial morphology of flank and other scales in several species belonging to both subgenera of *Serranochromis* (*sensu* Greenwood 1979; but see p. 37), all species of *Chetia*, and in different populations of the single *Pharyngochromis* species. In general I found a fairly high level of intrageneric variability, as well as some individual variability in the features noted by Lippitsch (1991: 99–100; figs D & E) *i.e.* ornamentation of the caudal field, and the presence of a soft caudal rim to the scale. Further studies will be necessary before the value of these features can be established, both at the group and lower levels of serranochromine taxonomy. However, another squamation feature noted and discussed by Lippitsch, namely the number of scale rows between the posterior orbital margin and the preoperculum, has proved of considerable value in reviewing generic level taxonomy within this group.

The generic or subgeneric status of Serranochromis Regan, 1920, and Sargochromis Regan, 1920, reconsidered.

In an attempt to revise the *Haplochromis* generic concept on phyletic lines, several so-called *Haplochromis* species were assigned, as a subgenus, to the genus *Serranochromis* (Greenwood, 1979). Since one of these species is the type of Regan's genus *Sargochromis* (*S. codringtoni* [Blg, 1908]) that name was resurrected for the new subgenus.

The principal argument for this taxonomic rearrangement was that the taxa included in the new concept of *Serranochromis* all share what appeared to be three derived features, *viz.* an increased number of abdominal vertebrae, higher gill-raker counts, and an increased number of branched rays in the dorsal fin (Greenwood, 1979: 299).

In the light of new data, especially those stemming from an increased knowledge of the genus *Chetia* (see p. 38) and, particularly, Lippitsch's (1991) observations on the different type of postorbital squamation patterns present in the two presumed subgenera, I would now revise my earlier action and recognise both *Serranochromis* and *Sargochromis* as distinct lineages, and thus accord each generic status. The reasons for that action are as follows.

Firstly, as Lippitsch (1991) noted, in *Serranochromis* but not in *Sargochromis* there are at least two, and often more, vertical rows of scales between the posterior orbital margin and the upper part of the preoperculum's ascending arm. In *Sargochromis* only a single row is present. A double row, however, also occurs in *Chetia* (personal observations, see below). Further investigation of both *Serranochromis* and *Chetia* reveals that the double and multiple scale row condition is correlated with underlying osteological and myological

characters that are not present in *Sargochromis* or *Pharyngochromis*, the two other serranochromines with only a single postorbital scale row. These correlated features are an increase in the relative size and bulk of the upper part of the *levator arcus palatini* muscle, and an anteriorly directed lengthening of the postorbital process from the sphenotic bone, particularly its ventral region associated with the origin of the muscle (see fig. 3 and fig. 8 in Greenwood, 1992). In *Sargochromis* and *Pharyngochromis* the muscle is relatively smaller, and the postorbital sphenotic process has the almost uniformly narrow form (Fig. 3) found in the generalised haplochromine skull (and, it may be added, the skulls of *Tylochromis* and *Heterochromis*, the genera thought to represent the least derived lineages of African cichlids; see Oliver, 1984, and Stiassny, 1989 & 1991).

The other reason for reconsidering the subgeneric status of *Sargochromis* is the increased information now available, especially for *Chetia* (see p. 38), which clearly indicates an extensive overlap in the gill-raker and dorsal fin-ray characters previously used (Greenwood, 1979) to define *Serranochromis* (then including *Sargochromis*). These characters, therefore, no longer can be considered synapomorphic for *Serranochromis* and *Sargochromis* alone.

With the elimination of those two characters, the only derived feature shared uniquely by *Serranochromis* and *Sargochromis* is the increased number of abdominal vertebrae. Against that presumed synapomorphy must be set the derived postorbital scale-row character shared only by *Serranochromis* (*sensu* Regan, 1920) and *Chetia*, which genera also share two apomorphic features not previously recognised. These are: (i) an increase in the range and modal number of caudal vertebrae (range 15–18, modes 16 and 17 in *Serranochromis*, range 15–17 modes 16 and 17 in *Chetia*, compared with ranges of 12–16 in *Sargochromis*, and 14–16 in *Pharyngochromis*, with modes of 14 and 15, and 15 in the genera respectively); (ii) an increase in the range and modal number of circumpenduncular scale, *viz.* 18–20, rarely 16, in *Serranochromis* and *Chetia*, neither taxon with a clear-cut modal number, as compared with 16 or 18 (mode 16) in *Sargochromis* and 15 or 16 (mode 15) in *Pharyngochromis*. The recognition of this feature as an apomorphy is based on the circumpenduncular counts for *Tylochromis* and *Heterochromis* (see above), where the range, and modes, are 15–16.

Thus, taking into account the presumed derived characters shared only by *Serranochromis* and *Chetia*, it would seem that the higher count of abdominal vertebrae in *Serranochromis* and *Sargochromis* should be treated as a homoplasy and not, as previously thought, an apomorphy indicating an immediate common ancestor for the two taxa. For that reason I agree with, and now formally act upon Lippitsch's (1991) conclusion that "It seems advisable . . . to recognise *Sargochromis* as a distinct genus. . .".

The possible relationship of *Sargochromis* within the serranochromines is discussed on p. 41, and a revised generic diagnosis is given on p. 42.

A few further comments need to be made about the genera *Serranochromis* and *Sargochromis*. The number of postorbital scale rows in certain *Serranochromis* species can be as high as four or five, and, as far as I can determine, the number of rows is relatively constant intraspecifically. At present insufficient information is available on possible inter- or intraspecific differences in scale ornamentation, or on such variation in the presence or absence of a soft free margin to the scales (see Lippitsch, 1991). The small sample of species I

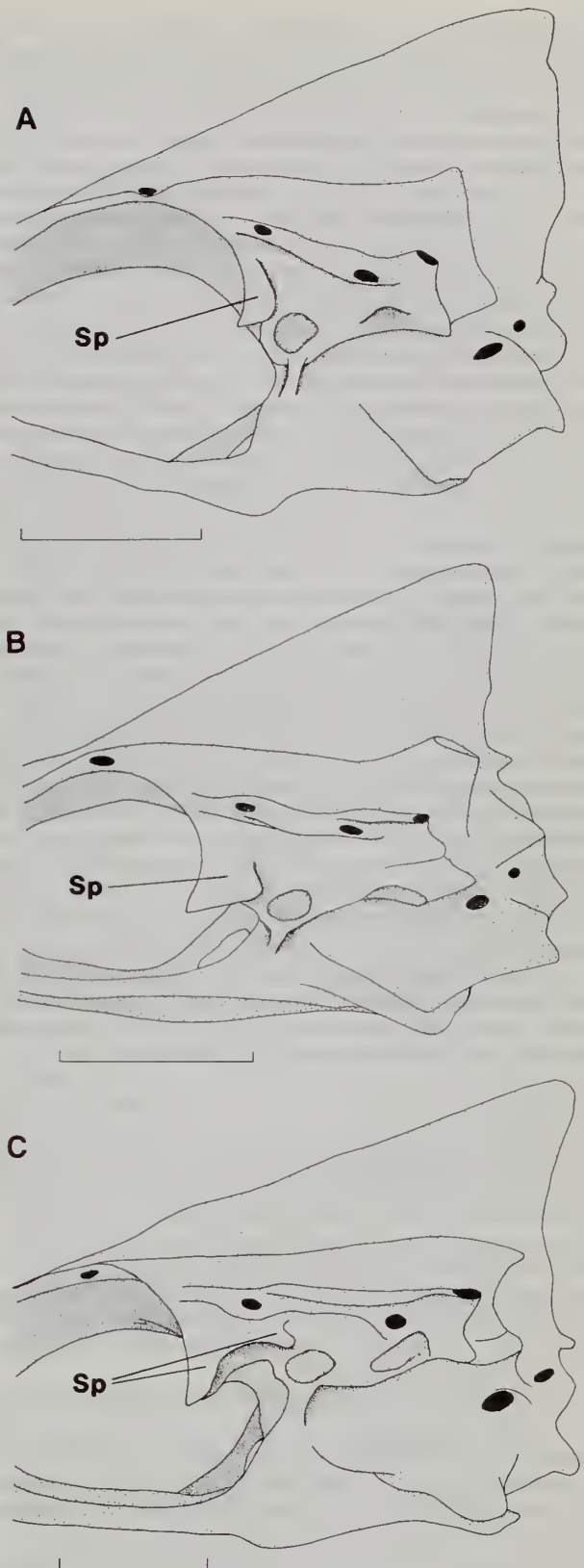


Fig. 3. Posterior portion of the neurocranium, in left lateral view, to show differences in the size of the sphenotic postorbital process (Sp.) in *Sargochromis*, *Chetia* and *Serranochromis*. A, *Sargochromis carlottae* (RUSI: 31204, 89 mm S.L.; B, *Chetia brevis* (AMG: P1422, 90 mm S.L.) and C, *Serranochromis macrocephalus* (RUSI: 24175, 112 mm S.L.) Scale bar = 5 mm.

have examined from the Okavango swamp and river system in Botswana seems to indicate that such variation may occur. A soft margin, for example, was absent in specimens of *Serranochromis thumbergi* and *S. longimanus*, but is present in *S. macrocephalus*. From the same samples some individual variability was noted both in the extent of the granular area on the caudal field of flank scales below the upper lateral-line, and the presence or absence of a granular area in at least some scales above that line. Apparent interspecific variation is also seen in the extent and nature of cheek, opercular and interopercular squamation patterns. The value of these features as a basis for intrageneric classification has, however, yet to be tested on a wider geographical and taxonomic basis.

A feature of *Serranochromis*, *Sargochromis* and *Chetia* noted in an earlier paper (Greenwood, 1979), where it was ranked as an apomorphy, is a reduction in the maximum number of inner tooth rows in both jaws to a single or irregularly double series. The new species, *S. altus*, described by Winemiller & Kelso-Winemiller (1991), is exceptional in having as many as six rows anteriorly, reducing to a single or double row posteriorly (the figures adjusted from Winemiller & Kelso-Winemiller who include the outer tooth row in their counts). These authors also note that the number of inner rows increases with growth "...in all species of *Serranochromis* that we have examined...". Their list of study material indicates, however, that only one other species, *S. angusticeps*, was studied, and that the maximum number of inner or outer rows in that species is three. Since museum specimens are often not fully representative of a species' full size-range, the possibility of growth related changes in the number of tooth rows should perhaps be treated, for the moment, as an open question. In that connection, however, it should be noted that in *Sargochromis*, one species, *Sargo. thysi*, has four inner rows in both jaws at a size when only one or two rows are present in other congeneric species.

Another dental feature in *Serranochromis*, one also shared with *Sargochromis*, (and probably *Chetia*), is for the two median teeth in the outer row of the inner tooth series to be enlarged and displaced anteriorly (Greenwood, 1984: 216; also see figs 3 & 8 in Trewavas, 1964). Amongst the sample of *Serranochromis* specimens examined, which included all species of the genus except *S. altus*. (see p. 35, and Greenwood, 1979 & 1984 for additional material), such tooth displacement occurs in most species but not in all individuals of a species. Its frequency of occurrence is lower in *Sargochromis* than in *Serranochromis*, and the condition is known from only one *Chetia* species (*C. gracilis*; see below and p. 39). Because of this inconstancy in its expression I would now consider the character more in the nature of a trend, albeit a derived one, rather than the trenchant synapomorphy recognised earlier (see Greenwood, 1984: 216).

A revised generic diagnosis for *Serranochromis* is given on p. 42, and the possible relationships of the genus are discussed on p. 40. To the list of included species published in Greenwood, 1979 (pp. 302–303) must be added *S. altus* Winemiller & Kelso-Winemiller (1991) from the Zambezi system.

Little need be added to previous accounts of the genus *Sargochromis*, type species *Paraillapia codringtoni* Blgr., 1908 (see Greenwood, 1979; 1984, in both papers the taxon treated as a subgenus) except to note that the species described as *Serranochromis* (*Sargochromis*) *gracilis* Greenwood (1984) from the Cunene river, is now considered to be a member of the genus *Chetia* (see p. 39). The transfer of this

species reduces to two the number of *Sargochromis* species having, relative to other congeneric taxa, slender lower pharyngeal bones with few and only partially molariform teeth, viz. *Sargochromis greenwoodi* (Bell-Cross) and *Sarg. coulteri* (Bell-Cross). The latter species, however, appears to show considerable variability in these features, with some individuals having noticeably coarser lower pharyngeal bones than do others, a feature invariably correlated with an increased number of molariform teeth (Greenwood, 1984: 217–221). As was discussed in that paper, the species level taxonomy of *Sargochromis* is far from satisfactory, so this seemingly intraspecific variability should only be accepted with some reservation (see also Greenwood, 1965 and Hoogerhoud, 1986).

In lacking a pronounced ventral expansion of its sphenotic postorbital process (see p. 37), the neurocranium in *Sargochromis* is immediately distinguishable from that of *Serranochromis* (see Fig 3; also comments in Greenwood, 1979: 303, and figs 13 & 16).

A list of *Sargochromis* species is given in Greenwood, (1979, pp. 304–305), and a revised generic diagnosis on p. 42 below.

The genus Chetia Trewavas, 1961

TYPE SPECIES: *Chetia flaviventris* Trewavas, 1961.

It has not proved possible to formulate a trenchant generic definition for *Chetia* since the taxon has yet to yield a single diagnostic autapomorphy. Its definition, therefore, is based on, as it were, negative features, namely those which exclude the five member species from inclusion in any of the three other serranochromine genera, especially *Serranochromis* with which *Chetia* has the greatest superficial and some detailed similarity. Thus, although *Chetia* shares with *Serranochromis* the apomorphy of two postorbital scale rows (see p. 36), a high number of caudal vertebrae (15–17, modes 16 or 17) and an increased number of circumpeduncular scales (18 or 20, rarely 16), it does not share with *Serranochromis* apomorphies of an increased number of abdominal vertebrae, (and as a consequence, an increase in the total number of vertebrae), nor the increased lateral-line scale count of that genus (35–41, a character probably correlated with the increased number of vertebrae). Neither do the two genera share the autapomorphic dental character of *Serranochromis*, namely the development of a totally unicuspid jaw dentition at a very small size; i.e., at some length, yet to be determined, less than 29 mm S.L.; see Greenwood, (1979: 300).

On the basis of that analysis, the simplest diagnosis for *Chetia* is: a *Serranochromis* lacking the apomorphic features of that genus (see also Greenwood, 1992: 49–50 and p. 43 below).

At the time of my earlier generic review (Greenwood, 1979), *Chetia* comprised two species, namely the type, *Chetia flaviventris*, and *Chetia brevis*, Jubb, 1968; the species coming from the Limpopo and Incomati river systems of South Africa respectively.

Based on Jubb's original description together with an examination of the holotype and two other *Chetia brevis* specimens, I excluded, in my 1979 paper, the species from *Chetia* and placed it, as *incertae sedis*, in the genus *Astatotilapia* (Greenwood, 1979: 284 & 307). That decision was based on three supposed features of *C. brevis*. (i) Jubb's (1968) description of the anal fin markings as ocelli, together with

his and my personal observations of their large size and restricted number (3 or 4) as compared with the small and numerous anal spots in other serranochromines (see p. 34), especially *Chetia flaviventris*. (ii) Jubb's (*op. cit.*) statement that the scales are ctenoid, and its implication that such scales are the predominant form. (iii) The presence of bicuspid teeth in the outer oral tooth rows of some specimens more than 100 mm S.L., contrasting with the situation in *Chetia flaviventris* where, on the information then available, few bicuspid teeth were thought to be present in fishes 71–85 mm S.L., and only unicuspid teeth occurred in specimens above that length.

Having now been able to examine colour-transparencies of live *C. brevis*, it is clear that the anal spots are not true ocelli (as defined on p. 34), but are large versions of the maculae found in other serranochromines, including *Chetia flaviventris*. The taxonomic significance to be attached to their large size, and small number, cannot yet be assessed. However, a wide size-range of anal maculae, their size negatively correlated with their number, occurs in the monotypic serranochromine genus *Pharyngochromis*, some individuals of which have spots as large as those in *Chetia brevis*.

The larger collection of *C. brevis* specimens now available, together with a re-examination of the entire type series, shows that Jubb's blanket description of the scales as ctenoid is somewhat misleading. As in *Chetia flaviventris*, the scales of *C. brevis* are cycloid above the lateral-line, and mostly cycloid below that level. A variable number, usually small, of ctenoid scales is present anteriorly on the flanks, such scales being most numerous in fishes less than 80 mm S.L. In other words, the same pattern as occurs in *Chetia flaviventris* is also found in *C. brevis*.

An examination of larger samples of both *C. flaviventris* and *C. brevis* also revealed that bicuspid teeth can be present in individuals of *C. flaviventris* up to a standard length of 90 mm, and that true unicuspid teeth as well as very weakly shouldered (almost unicuspid) teeth occur in *C. brevis* specimens between 80 and 90 mm S.L. This situation severely weakens my third reason (see above) for excluding *C. brevis* from the genus *Chetia*.

Furthermore, the presence of two vertical rows of postorbital scales in both *Chetia brevis* and *C. flaviventris* (see p. 36), a feature previously overlooked by all workers, provides additional evidence for returning the species 'brevis' to the genus in which it was originally, and I now acknowledge correctly placed by Jubb (1968).

Since 1979 another two species have been included in the genus, namely the taxon *Chetia mola* described by Balon & Stewart (1983) from the Zaire river system, and *Haplochromis welwitschi* (Blgr.) from Angola (see Greenwood, 1979 & 1984).

Chetia mola differs from all other congeneric species in having a greatly enlarged lower pharyngeal bone with a heavily molarized dentition (see fig. 12 in Balon & Stewart 1983), a type of pharyngeal mill more usually associated with species of *Sargochromis*. However, unlike members of that genus, *C. mola* has a double or sometimes triple row of postorbital scales, and a lower number of abdominal vertebrae.

To the existing four species of *Chetia*, I would now add a fifth, a species from the Cutato river, Angola, originally described (Greenwood, 1984) as *Serranochromis* (*Sargochromis*) *gracilis*. The reasons for this transfer are the double row of postorbital scales in 'gracilis', the persistence

of compressed, bi- and weakly bicuspid teeth in the outer tooth row of both jaws in specimens over 100 mm S.L. and of tricuspid teeth in the inner tooth rows in such individuals (see Greenwood, 1984: 227, and above), and the presence of only 15 abdominal vertebrae, a combination of derived and plesiomorphic characters not occurring in any known *Sargochromis* or *Serranochromis* species.

On the basis of comparisons with the few specimens available, *Chetia gracilis* (n=2) differs from the only other *Chetia* species recorded from southwestern Africa, *C. welwitschi* (n=5), in having a narrower interorbital width (18.2–18.6 cf 21.0–23.3% of head length in *C. welwitschi*), a larger eye (25.0–25.6, cf 18.6–22.25% head; the effects of allometry are unlikely to account for this difference since the two samples overlap in the size range of individuals represented), and a shallower cheek (22.7–23.3 cf 32.0–33.3% head). The lower pharyngeal bone in *C. gracilis* is somewhat stouter, and its median teeth coarser than in *C. welwitschi* (cf figs 19 & 20 in Greenwood, 1984).

In its morphometric and meristic features, *C. gracilis* closely resembles *C. flaviventris* and *C. brevis*, species respectively from the Limpopo and Incomati river systems in South Africa. From *Chetia brevis*, *C. gracilis* is distinguished by its narrower interorbital width (18.2–18.6 cf 23.0–26.0% head length), and from *C. flaviventris*, especially when specimens of approximately the same size are compared, by its shallower cheek (22.7–23.3 cf 25.5–33.6% head). It also seems likely that, when the effects of allometric growth are taken into account, the eye diameter is greater in *C. gracilis* than in *C. flaviventris*. The teeth in the median row of the lower pharyngeal bone of *C. gracilis* are coarser and stouter than those of *C. flaviventris*, in that respect being more like the teeth in *C. brevis* (cf fig. 19 in Greenwood, 1984, fig. 19 in Greenwood, 1974, and fig. 4B in Jubb, 1968).

Regrettably, apart from *Chetia flaviventris* (see du Plessis & Groenewald, 1953; Trewavas, 1961) and *C. mola* (see Balon & Stewart, 1983; fig. 10b) little or nothing is known about the live coloration of the other *Chetia* species.

A revised generic diagnosis for *Chetia* is given on p. 43.

Included species:

Chetia flaviventris Trewavas, 1961. Limpopo river system.

Chetia brevis Jubb, 1968. Incomati river system

Chetia mola Balon & Stewart, 1983. Luongo river, Zaire system.

Chetia welwitschi (Boulenger), 1898. Cunene and Zaire river drainage systems, Angola (see Greenwood, 1979).

Chetia gracilis (Greenwood), 1979. Cutato river (Cubango drainage system), Angola.

The genus *Pharyngochromis* Greenwood, 1979.

TYPE SPECIES: *Pelmatochromis darlingi* Boulenger, 1911.

A detailed revision of this monotypic genus, together with an annotated synonymy, has been published recently (Greenwood, 1992). Three nominal species all classified in the genus *Haplochromis* since Regan's revision of 1922 (or in one case, *Pharyngochromis*), viz. *Pelmatochromis darlingi* Boulenger, 1911; *Chromis jallae* Boulenger, 1896, and *Pelmatochromis multiocellatus* Boulenger, 1913, are now treated as junior synonyms of the single *Pharyngochromis* species, *P. acuticeps* (Steindachner) 1866.

There are some indications that *P. acuticeps* could be

considered either as a superspecies composed of several topospecies or as an assemblage of evolutionary species, but no clear-cut features allowing a formal taxonomic division of the taxon can be identified (see Discussion in Greenwood, 1992).

Anatomically and morphologically, *Pharyngochromis* is the least derived member of the serranochromines. Its sole autapomorphic feature is the higher position occupied by the posterior scales of the upper lateral-line series relative to the base of the dorsal fin (see Greenwood, 1992). The last five to seven (rarely four or eight) pored scales in that series are separated from the dorsal fin base by only one large and one much smaller scale. In the other serranochromine genera only the last one or two pored scales are separated from the fin base in this way, the other posterior scales having at least two large scales of equal size interposed between them and the fin base (see Greenwood, 1979 & 1992).

In most *P. acuticeps* specimens (from all localities) the lower pharyngeal bone is slightly enlarged, and some of its median row teeth, which are always coarser than their lateral congeners, have molariform or submolariform crowns (Greenwood, 1992, fig. 7). There is, however, considerable individual variability in the degree to which this bone is enlarged and its teeth are molarized. In these respects, *P. acuticeps* resembles certain *Sargochromis* species, particularly *S. coulteri* (Bell-Cross) and *S. greenwoodi* (Bell-Cross). But, since the two genera differ in several other features, I would consider this resemblance to be homoplastic and not, as Trewavas (1961: 9) suggested, one of phylogenetic significance.

If the serranochromines are a monophyletic lineage, (see p. 41) their recent common ancestor could well have resembled the extant *Pharyngochromis acuticeps*, except for the incipient hypertrophy of the pharyngeal jaws in the latter.

Pharyngochromis acuticeps has a very wide distribution which includes the Zambezi and Save-Runde river systems, the Okavango river and its delta swamps, Lake Calundo, the Lucala river (Quanza drainage) and some unidentifiable localities in Angola. Records of the species (as *Haplochromis darlingi*) from the Limpopo river system (Jubb, 1967, repeated in Greenwood, 1979) are now known to be erroneous and probably based on the misidentification of small *Chetia flaviventris* specimens.

A revised generic diagnosis of *Pharyngochromis* is given in Greenwood (1992:48) and on p. 42 below.

CONCLUSION

The phyletic relationships of the serranochromines

The difficulties encountered in determining both the inter- and intrarelations of these fishes were discussed in two previous papers (Greenwood, 1979 & 1992), as was Trewavas' earlier (1964) tentative scheme of their relationships. Basically the problem lay, and still lies, in establishing whether or not the group is of monophyletic origin.

One of the two features unifying the serranochromines, the non-ocellate anal fin markings, is probably a plesiomorphic character, perhaps representative of a stage in the evolution of true ocelli and one in which the markings, unlike true ocelli, are not confined to males (Greenwood, 1979; Oliver,

1984). However, the possible function of anal maculae as egg-dummies (*sensu* Wickler, 1962; 1963), or even if they play any part in reproductive behaviour (Hert, 1989), have yet to be determined. There is also the possibility that non-ocellar anal markings have evolved more than once within the haplochromine cichlids (*sensu lato*), as their presence in species of *Thoracochromis* (Greenwood, 1979, 1984) could suggest. (Alternatively, *Thoracochromis* and the serranochromines may be more closely related than other morphological and anatomical evidence would indicate.) In this context, Eccles & Trewavas', (1989: 27) observations on three species of the endemic Malawi genus *Aulonocara* are pertinent. One of these species has simple spots, a second has spots surrounded by a contrasting border, and the third no markings at all, although the fin has a pale border. Since *Aulonocara* has a number of distinctive anatomical autapomorphies, this situation certainly suggests that not only have different kinds of anal fin markings evolved more than once but have done so within a single genus.

Another aspect of the problem involving phylogeny and anal markings is Oliver's (1984: 108) suggestion that haplochromines with multiple non-ocellar spots, together with those having true ocelli, comprise a monophyletic assemblage whose members are more closely related to one another than to any species with what he considers to be the plesiomorphic condition of anal maculae, namely spots indistinguishable from those on the other unpaired fins, especially the dorsal fin. That hypothesis has yet to be tested by the identification of suitable congruent and derived features characterizing the two supposed lineages, and raises questions about the significance of the seemingly unique anal marking of *Pseudocrenilabrus* species (Greenwood, 1989).

All in all, the current evidence for anal fin markings being of value in reconstructing phylogenies is not encouraging, particularly at the taxonomic levels under consideration here. For that reason I cannot agree with Eccles & Trewavas' (1989) use of the feature as grounds for suggesting a close relationship between the fluviatile serranochromines and most of the endemic haplochromines of Lake Malawi. While agreeing that non-ocellar anal spots are plesiomorphic features, these authors believe that the absence of true ocelli in the two groups "...combined with the geomorphological history of the region ... may be accepted as evidence for the relationship of the Malawian group of species with the haplochromines of the Zambezi area" (*i.e.*, with *Serranochromis*, *Sargochromis* and *Pharyngochromis*; *Chetia* has not been recorded from the Zambesi system). Certainly the similarity in anal fin markings would seem to support the intuitive feeling that the two groups could be related (see p. 34), and thus encourage a search for other characters to confirm or refute that impression, but in itself I would not rate it as 'evidence'.

The second morphological character used to define the serranochromines, *i.e.* cycloid scales above the lateral line and a preponderance of such scales below that level, is, I would argue, a derived condition (Greenwood, 1979; see also Oliver, 1984; Lippitsch, 1991). Nevertheless, it is not clearly an autapomorphic feature of the serranochromines. For example, in the Lake Malawi haplochromines mentioned above, there is also a marked reduction in scale ctenoidy, but here, although scales above the lateral-line, like those in the serranochromines, are cycloid, the ctenoid scales occurring below that level are confined to the posterior part of the body and not the anterior part as in serranochromines. In a

phylogenetic context how are these similarities and differences, to be evaluated?

Again, a pattern of reduced ctenoidy like that in the serranochromines occurs in some but not all species of *Thoracochromis* (Greenwood, 1979; 291; 1984:192 & 200), a genus in which, apparently, there are both true ocellar and non-ocellate types of anal fin markings (see above), but with both kinds occurring only in males. Possibly the 'genus' *Thoracochromis* is polyphyletic and that some of its species should be included in the serranochromine assemblage. Here, as is so often the case, one is hampered both by a paucity of detailed information on live coloration and the relatively few specimens available for anatomical and morphological studies.

Another difficulty, linked with lack of information, lies in the possibility that further research could establish that there really is a close phylogenetic relationship between the serranochromines and certain haplochromines of Lake Malawi. In that eventuality, it is possible that the nearest relative of one or more of the fluviatile serranochromine taxa is to be found in the lake's fauna, thus rendering the serranochromines, as currently conceived, either a para- or a polyphyletic group.

Although at present the monophyly of the serranochromines cannot be established or refuted, it is possible to construct, on the basis of shared derived features, a tentative intragroup taxonomy.

As compared with *Pharyngochromis*, the genera *Chetia*, *Serranochromis* and *Sargochromis* all share two derived features (see Liem, 1991) associated with the upper jaw skeleton, viz an increase in the shank length of the maxilla relative to its pre-shank length, and an increase in the length of the alveolar process of the premaxilla relative to the length of the entire ascending process of that bone (see Methods). In *Pharyngochromis* the preshank portion of the maxilla is from 1.2–1.3 times longer than its shank length, whereas in *Chetia* and *Sargochromis* the two parts are of equal length (with, in some *Sargochromis* species the preshank portion slightly shorter) and in *Serranochromis* the shank is noticeably longer (as much as 1.3 times so). In *Pharyngochromis* the length of the alveolar process of the premaxilla's ascending process is 60–66% of the length of the entire ascending process; in *Sargochromis* it is from 69–76%, in *Chetia* 73–77% and in *Serranochromis* 73–83%.

Neither of these ratios, either inter- or intragenerically, appears to be influenced by the size of the 17 specimens examined, all in the size range 79–410 mm S.L. and representing ten species.

On the basis of those two characters, a *Pharyngochromis* and a *Chetia* – *Serranochromis* – *Sargochromis* subgroup can be recognised within the serranochromines. Both these derived features are the only ones shared by the three latter genera (the increased number of abdominal vertebrae used previously to unite *Sargochromis* and *Serranochromis* in a single genus [Greenwood, 1979] is now thought to be a homoplasy; see p. 37).

Chetia and *Serranochromis* both share three derived features not found in *Sargochromis* or in *Pharyngochromis* viz. (i) an increased modal number of caudal vertebrae (range 15–17, modes 16–17 in *Chetia*, and 15–18, modes 16 and 17 in *Serranochromis*) compared with *Sargochromis* (range 12–16, modes 14 and 15) and *Pharyngochromis* (range 14–16, mode 15). (ii) Two or more vertical rows of postorbital scales (cf a single row in *Sargochromis* and *Pharyngochromis*, see p. 36). (iii) An increased number of scale rows around the caudal

peduncle, i.e. 18–20, rarely 16, compared with 16–18 rarely 15, (mode 16), in *Sargochromis*, and 15 or 16 (mode 15) in *Pharyngochromis*.

On the basis of those three derived characters, and using the term 'sister taxon' without any phylogenetic implications, then, within the serranochromines, *Pharyngochromis* is the sister taxon to the group *Sargochromis*, *Chetia* and *Serranochromis*, and within that latter group, *Sargochromis* is the sister taxon of *Serranochromis* and *Chetia* combined.

That scheme bears, in broad outline, a close resemblance to Trewavas's (1964) diagram suggesting the interrelationships of *Serranochromis*, a scheme based essentially on lateral-line and dorsal fin ray counts (which may, of course, be correlated, in part, with the vertebral counts used here) and certain characteristics of the pharyngeal jaws.

When comparing the two schemes, allowances must be made for the fact that two of Trewavas' *Haplochromis* species (*lucullae* and *darlingi*) are now treated as synonyms of *Pharyngochromis acuticeps* (Greenwood, 1992), that the status of *H. angolensis*, *H. humilis* and *H. toddi* is uncertain or unknown (Bell-Cross, 1975, Greenwood, 1979), and that *H. welwitschi* is now considered to be a species of *Chetia* (see p. 39). Also, the two *Haplochromis* species, *mellandi* and *frederici*, placed in limbo between the genera *Haplochromis* and *Sargochromis* in Trewavas' diagram, are now included in *Sargochromis* (Bell-Cross, 1975; Greenwood, 1979 and above p. 37), as is *Haplochromis carlottae*.

Trewavas (*op. cit.* 9–10) superimposed on her diagram a tree indicating the possible phylogenetic relationships of the taxa, both inter- and intragenerically. It is here that our views would not coincide, mainly because I do not think there is the evidence, based on cladistic methodology, to justify the relationships proposed, even at an intergeneric level (see p. 40). Certainly there are no features justifying Trewavas' (*op. cit.* 10) suggestion that *Serranochromis* is a diphyletic and gradal taxon or that a cladal grouping would recognise *Chetia*, *Serranochromis robustus* and *S. thumbergi* on the one hand, and *Chetia welwitschi* (Trewavas' *Haplochromis welwitschi*), and the remaining *Serranochromis* species on the other. Nor can I accept Trewavas' uncertainty about the separation of *Sargochromis codringtoni*, *mellandi*, *carlottae* and *greenwoodi* (as *Haplochromis frederici* in her scheme; see Bell-Cross, 1975) from the '*Haplochromis*' (i.e. *Pharyngochromis*,) root of her tree (see Greenwood, 1979, 1992 and above). A truly phylogenetic assessment of the groups' relationships must, as discussed on p. 36, await the results from further and preferably multidisciplinary research into the systematics of all the serranochromine species, and those many Malawi species that Eccles & Trewavas (1989: 21) have placed in their *Pharyngochromis* – *Chetia* – *Serranochromis* group.

Generic key and diagnoses

A single row of scales between the posterior orbital margin and the vertical limb of the preoperculum A
Two or more scale rows between the posterior orbital margin and the vertical limb of the preoperculum B

A. Last 2 or 3 pored scales in the upper lateral-line series separated from the dorsal fin base by not less than two scales of approximately equal size A(i) *Sargochromis*
Last 5 to 7 (rarely 4 or 8) pored scales in the upper lateral line separated from the dorsal fin base by one large and one small scale A(ii) *Pharyngochromis*

A(i):

Abdominal vertebrae [15] 16–18 [19], modes 16 and 17; caudal vertebrae 12–16, modes 14 and 15; total number of vertebrae 28–32 (mode 31).

Dorsal fin with 13–16, modes 15 and 16, spinous rays and 11–16, modes 12 and 13, branched rays. Anal fin with 3 spines and 8–11, mode 9, branched rays. Caudal fin truncate, subtruncate or almost rounded.

Scales in the lateral series 28–34, modes 30 and 31. Cheek with 3–6 horizontal rows. [15] 16–18, mode 16, scales around the caudal peduncle.

Gill-rakers in the outer series on the first ceratobranchial 9–15, modes 12 and 13.

Outer series of teeth in both jaws composed mainly of unequally bicuspid teeth in fishes <150 mm S.L., but predominantly of unicuspid in larger specimens. Inner series of jaw teeth, except in one species, arranged in a single or double series anteriorly and anterolaterally, reducing to a single row posterolaterally; in the exceptional species there are 4 rows anteriorly and anterolaterally, and a single row posterolaterally.

Pre-shank length of the maxilla equal to, or slightly shorter than the shank-length (see p. 34). Height of the premaxillary alveolar process 69–76% of the height of the entire ascending process (see p. 35). For comments on neurocranial morphology and other osteological features (including the lower pharyngeal bone and its dentition, see text and figures in Bell-Cross (1975) and Greenwood (1979: 303–305, figs. 16–18; and 1984: 216–225, figs. 12–17).

Lower pharyngeal bone hypertrophied in the majority of species, greatly so in some, but only slightly enlarged in two species. The extent and degree to which the dentition of this bone is molarized is positively correlated with the degree of the bone's hypertrophy. In species with slightly enlarged bones only a few molar-like or submolariform teeth are present, and are confined to the median tooth rows. The ventral outline of the bone's anterior keel is almost straight and rarely extends below a horizontal drawn through the deepest point on the bone's ventral surface below the dentigerous area. In specimens with a greatly enlarged lower pharyngeal bone, however, the ventral margin of the keel extends a little below that level (see figs 12–17 in Greenwood, 1984).

Anal fin spots small and numerous (as many as 40). *Sargochromis*

A(ii):

Abdominal vertebrae [13] 14 or 15 [16], mode 14; caudal vertebrae 14–16, mode 15; total number of vertebrae 28–31, mode 30.

Dorsal fin with 14–16, mode 15, spinous rays and [10] 11–13 [14] branched rays. Anal fin with 3 spines and 8 or 9 branched rays (no distinct modal number). Caudal fin distinctly truncate, subtruncate or almost rounded.

Scales in the lateral series [30] 31–36, mode 33, modal range 32–34. Cheek with [3] 4–6 horizontal rows. 15, rarely 16, scales around the caudal peduncle.

Gill-rakers in the outer row on the first ceratobranchial 7–12, modes 9 and 10.

Outer series of jaw teeth composed of unequally bicuspid teeth in fishes <80 mm S.L., although some unicuspid can be found in larger fishes within that length range. Unicuspid become the predominant form in fishes >90 mm S.L. Inner series of teeth, in both jaws, arranged in 1–3 rows anteriorly

and anterolaterally, reducing to a single row posterolaterally. The number of inner rows anteriorly appears to be positively correlated with an individual's size.

Pre-shank length of the maxilla clearly greater than the shank length (see p. 34), *i.e.* about 1.2–1.3 times longer. Height of premaxillary alveolar process 60–66% of the height of the entire ascending process. For comments on neurocranial form and other osteological features, see Greenwood (1992).

Lower pharyngeal bone in most individuals showing a slight degree of hypertrophy. In specimens over 50 mm S.L., the median rows of lower pharyngeal teeth are composed of noticeably coarser teeth than those situated laterally, and some can have submolariform crowns; the degree of molarization is most marked in fishes over 100 mm S.L. Irrespective of the degree to which the lower pharyngeal bone is enlarged, its anterior keel is deep, with a curved ventral outline whose deepest point lies below a horizontal drawn though the deepest point of the ventral surface underlying the dentigerous part of the bone (*cf Sargochromis* above); see fig. 7, Greenwood, 1992.

Anal fin spots of variable size and number, from as few as 3 or 4 large spots to as many as 19 small ones *Pharyngochromis*.

B. 16–18 (rarely 15 or 19) abdominal vertebrae; inner and outer rows of jaw teeth composed entirely or mostly of unicuspid in fishes over 30mm S.L. (and possibly in smaller individuals as well) B(i) *Serranochromis*

14 or 15 abdominal vertebrae; many bicuspid (or weakly bicuspid) teeth present in the outer tooth rows of both jaws in fishes as large as 80 mm S.L. B(ii) *Chetia*

B(i)

Abdominal vertebrae [15] 16–18 [19], modes 16 and 17; caudal vertebrae [15] 16–18, modes 16 and 17; total number of vertebrae 31–36 (no distinct modes).

Dorsal fin with 13–18, modes 15 and 16, spinous rays, and 13–16, modes 14, 15 and 16, branched rays. Anal fin with 3 spines and 9–13, modes 10 and 11, branched rays. Caudal fin subtruncate or almost rounded.

Scales in the lateral series [34] 35–41, no distinct modes. Cheek with 3 (rarely) to 11 horizontal rows (modally 5–9 rows). 18–20 scales around the caudal peduncle (no distinct mode).

Gill-rakers in the outer series on the first ceratobranchial [8] 9–13, modes 10, 11 and 12.

Outer and inner series of jaw teeth composed of unicuspid in specimens over 30 mm S.L. Inner series of both jaws, in all but one species, arranged in a single or double row (rarely 3 rows) anteriorly and anterolaterally, and a single row posterolaterally. In the exceptional species there are as many as six rows anteriorly and anterolaterally, reducing to a single or double row posterolaterally.

Pre-shank length of the maxilla shorter than its shank-length (see p. 34), which is *ca* 1.2–1.3 times longer than the pre-shank portion. Height of the premaxillary alveolar process 73–82% of the height of the entire ascending process (see p. 34). For comments on the neurocranium and other osteological features see Greenwood (1979: 299–302; figs. 13–15) and Trewavas (1964).

Lower pharyngeal bone slender, its dentigerous surface elongate and narrow (see figures in Trewavas, 1964, and Greenwood, 1979). No molariform pharyngeal teeth; even

those teeth in the median rows are only a little coarser than the other and fine teeth on the bone.

Anal fin spots small and numerous (as many as 40) *Serranochromis*

B(ii):
Abdominal vertebrae 14 or 15 (no distinct mode); caudal vertebrae 15–17, modes 16 and 17; total number of vertebrae 30–32, mode 31.

Dorsal fin with 14 or 15, mode 15, spinous rays and 10–13, modal range 11 or 12, branched rays. Anal fin with 3 spines and 7–10 branched rays (no distinct mode). Caudal fin truncate to subtruncate.

Scales in the lateral series 32–35, modal range 32–34. Cheek with 4–6, modes 5 and 6, horizontal rows; 18 or 20 (rarely 16) scales around the caudal peduncle.

Gill rakers in the outer series on the first ceratobranchial 9–11, modes 10 and 11.

Outer series of teeth in both jaws composed mainly of unequally bicuspid, but with a few unicuspid or weakly shouldered bicuspid present, in fishes < 80 mm S.L.; however, in some specimens of *Chetia flaviventris*, unicuspid predominate in fishes in the upper part of that size-range. In specimens >100 mm S.L. the outer teeth are predominantly unicuspid, with a few very weakly shouldered bicuspid also present. Inner tooth rows of both jaws arranged in a double series anteriorly and anterolaterally, reducing to a single row laterally and posteriorly. In one species (*Chetia gracilis*) at least some specimens have the two anterior median teeth in the outer row of inner teeth enlarged and displaced anteriorly relative to the other teeth in that row.

Pre-shank length of the maxilla equal to its shank length (see p. 34). Height of the premaxillary alveolar process 73–77% of the height of the entire ascending process (see p. 35).

Except in one species, the lower pharyngeal bone is not enlarged, and the median tooth rows are composed of bicuspid teeth only a little coarser than their lateral congeners. In the exceptional species, *C. mola* (see Balon & Stewart, 1983; fig. 12) the bone is greatly hypertrophied and massive, with all but a few of its laterally situated teeth enlarged and molariform or submolariform.

Anal fin spots usually small and fairly numerous (7–15) but in one species, *C. brevis*, there are only 3 or 4 large spots. *Chetia*

ACKNOWLEDGEMENTS. To Paul Skelton go my sincere thanks for the many discussions we have had on the subject of serranochromine cichlids, and for providing me with excellently documented material and field data. Once again it is a pleasure to thank Mike Bruton, Director of the J.L.B. Smith Institute for his hospitality and the fine working facilities provided by the Institute, Huibre Tomlinson for her tenacity and good humour when producing the typescript, and Elaine Heemstra for her excellent art-work.

REFERENCES

Balon, E.K. & Stewart, D.J. 1983. Fish assemblage in a river with unusual gradient (Luongo, Africa — Zaire system), reflections on river zonation, and description of another new species. *Environmental Biology of Fishes* 9 (3–4) 225–252.
Bell-Cross, G. 1975. A revision of certain *Haplochromis* species (Pisces :

Cichlidae) of Central Africa. *Occasional papers of the National Museums and Monuments of Rhodesia*, Series B, Natural Sciences 5(7): 405–464.
du Plessis, S.S. & Groenewald, A.A. 1953. The kurper of Transvaal. *Fauna & Flora, Transvaal Provincial Administration* 3: 35–43.
Eccles, D.H. & Trewavas, E. 1989. *Malawian cichlid Fishes. The classification of some haplochromine genera*. 335pp. Lake Fish Movies, Hereten, Germany.
Greenwood, P.H. 1965. Environmental effects on the pharyngeal mill of a cichlid fish, *Astatoreochromis alluaudi*, and their taxonomic implications. *Proceedings of the Linnean Society of London* 176: 1–10.
— 1979. A review of the pharyngeal apophysis and its significance in the classification of African cichlid fishes. *Bulletin of the British Museum (Natural History)*, Zoology 33: 297–323.
— 1979. Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces, Cichlidae) and related taxa. Part I. *Bulletin of the British Museum (Natural History)*, Zoology 35: 265–322.
— 1980. Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces, Cichlidae) and related taxa. Part II *Bulletin of the British Museum (Natural History)*, Zoology 39: 1–101.
— 1981. *The Haplochromine Fishes of the East African Lakes*. p. 839. British Museum (Natural History) London & Kraus International Publications, Munich.
— 1984. The haplochromine species (Teleostei, Cichlidae) of the Cunene and certain other Angolan rivers. *Bulletin of the British Museum (Natural History)*, Zoology 47: 187–239.
— 1986. The pharyngeal apophysis on the base of the skull in cichlid fishes. A reply to Trewavas (1985). *Netherlands Journal of Zoology* 36 (4): 562–4.
— 1987. The genera of pelmatochromine fishes (Teleostei, Cichlidae). A phylogenetic review. *Bulletin of the British Museum (Natural History)*, Zoology 53: 139–203.
— 1989. The taxonomic status and phylogenetic relationships of *Pseudocrenilabrus* Fowler (Teleostei, Cichlidae). *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology, Grahamstown* No. 54: 1–16.
— 1992. A revision and redescription of the monotypic cichlid genus *Pharyngochromis* (Teleostei, Labroidae). *Bulletin of the British Museum (Natural History)*, Zoology 58: 37–52.
Hert, E. 1989. The function of egg-spots in an African mouthbrooding cichlid fish. *Animal Behaviour* 37: 726–732.
Hoogerhoud, R.J.C. 1986. Taxonomic and ecological aspects of morphological plasticity in molluscivorous haplochromines (Pisces, Cichlidae). *Musee Royal de L'Afrique Centrale, Tervuren; Annales Sciences Zoologique* 251: 131–4.
Jubb, R.A. 1967. *The Freshwater Fishes of Southern Africa* vii + 248 pp. Balkema, Cape Town.
— 1968. A new *Chetia* (Pisces, Cichlidae) from the Incomati River system, Eastern Transvaal, South Africa. *Annals of the Cape Provincial Museums (Natural History)* 6 (7): 71–76.
Konings, A. 1991. *Cichlid and all other fishes of Lake Malawi* 495 pp. T.F.H. Publications, New Jersey.
Ladiges, W. 1964. Beiträge zur Zoogeographie und Oekologie der Süßwasserfische Angolas. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 61: 221–272.
Liem, K.F. 1991. Functional morphology. pp. 129–150. In: Keenleyside, M. (Ed.) *Cichlid Fishes*. Chapman & Hall, London.
Lippitsch, E. 1991. Comparative investigation on scale characters in cichlids. *Musee Royal de L'Afrique Centrale, Tervuren; Annales Sciences Zoologique* 263: 97–102.
Oliver, M.K. 1984. *Systematics of African cichlid fishes: determination of the most primitive taxon, and studies of the haplochromines of Lake Malawi* (Teleostei, Cichlidae). Ph.D. Thesis, Yale University.
Poll, M. 1967. Contribution a la faune ichthyologique de l'Angola. *Museu do Dundo, Publicacoes Culturais* No. 75: 1–381.
— 1986. Classification des Cichlidae du lac Tanganika. Tribus, genres et espèces. *Académie Royale de Belgique; Mémoires de la Classe des Sciences, collection in 8°, 2e series*, 45 (2): 1–163.
Regan, C.T. 1920. The classification of the fishes of the family Cichlidae. I The Tanganyika genera. *Annals and Magazine of Natural History* (9)8: 632–639.
— 1922. The classification of the fishes of the family. Cichlidae. II. On African and Syrian genera not restricted to the Great Lakes. *Annals and Magazine of Natural History* (9)10: 249–264.
Skelton, P.H. 1993. *A complete Guide to the Freshwater Fishes of Southern Africa*. Southern Book Publishers, Halfway House, South Africa. (In press).
Stiassny, M.L.J. 1989. A taxonomic revision of the African genus *Tylochromis* (Labroidae, Cichlidae); with notes on the anatomy and relationships of the group. *Musee Royal de L'Afrique Centrale, Tervuren; Annales Sciences Zoologiques* 258: 1–161.
— 1990. *Tylochromis*, relationships and the phylogenetic status of the African Cichlidae. *American Museum Novitates* no. 2993: 1–14.
Trewavas, E. 1961. A new cichlid fish in the Limpopo basin. *Annals of the South African Museum* 46(5): 53–56.

- 1964. A revision of the genus *Serranochromis* Regan (Pisces, Cichlidae). *Musee Royal de l'Afrique Centrale, Tervuren; Annales, serie in -8^e, Sciences Zoologique* no. 125: 1-58.
- 1983. *Tilapiine fishes of the genera Sarotherodon, Oreochromis and Danakilia* viii + 583p. British Museum (Natural History), London.
- Wickler, W. 1962. Ei-Attrappen und Maulbrüten bei Afrikanischen Cichliden. *Zeitschrift für Tierpsychologie* 19(2): 129-164.
- 1963. Zur Klassifikation de Cichlidae, am Beispiel der Gattungen *Tropheus*, *Petrochromis*, *Haplochromis* und *Hemihaplochromis* n.gen. (Pisces, Perciformes). *Senckenbergiana Biologica* 44(2): 83-96.
- Winemuller, K.O. & Kelso-Winemiller, L.C. 1991. *Serranochromis altus*, a new species of piscivorous cichlid (Teleostei:Perciformes) from the upper Zambezi river. *Copeia* 3: 675-686.